

**STRUCTURE OF SOME EPIDERMAL GLANDS IN THE
MYRMECOPHILOUS BEETLE ADRANES TAYLORI
(COLEOPTERA: PSELAPHIDAE)**

W. B. HILL, R. D. AKRE, AND J. D. HUBER

Reprinted from the
JOURNAL OF THE KANSAS ENTOMOLOGICAL SOCIETY
Vol. 49, July, 1976, No. 3
pp. 367-384
Made in United States of America

STRUCTURE OF SOME EPIDERMAL GLANDS IN THE MYRMECOPHILOUS BEETLE *ADRANES TAYLORI* (COLEOPTERA: PSELAPHIDAE)¹

W. B. HILL, R. D. AKRE, AND J. D. HUBER^{2,3}

ABSTRACT

Six morphologically distinct types of epidermal gland cells and their distribution are described from the pterothorax and abdomen of *Adranes taylori*. Four types are intimately associated with various groups of trichomes possessed by this beetle. All six types of gland cells are variations of class 3 gland cells.

Types 1 and 2 resemble in morphology the sex pheromone secreting gland cells of male *Harpobittacus*. Types 3a + b and 4a + b are similar to cells 2a + b in the defense glands of *Eleodes* and the cells comprising the pygidial glands of *Bledius*. Cell types 5 and 6 were not investigated in detail. However, type 6 is presumed to have a lubricating function due to its distribution.

Studies on *Adranes lecontei* Brendel (Park, 1942), *Claviger testaceus* Preysseler (Kruger, 1910), and *Adranes taylori* Wickham (Akre and Hill, 1973) have shown the trichomes, tufts of golden-yellow hairs, possessed by these beetles are highly attractive to their ant hosts. These beetles belong to the Clavigerinae (Pselaphidae) which as a group are obligate myrmecophiles or ant guests, and are all highly modified for their close relationship with their host (Akre and Hill, 1973; Park, 1942).

An adaptation common to many coleopterous inquilines is the development of epidermal glandular systems that produce substances attractive to and consumed by the host, that mimic the colony odor of the host, or that act in some other manner resulting in acceptance of the inquiline by the host (Wilson, 1971). These glands or gland cells are frequently associated with trichomes that aid in the dispersal of the secretion. Glands of this nature have been described from several myrmecophiles and termitophiles (Jordan, 1913; Kruger, 1910; Seyfried, 1928; Pasteels, 1968; Pasteels and Kistner, 1970).

Adranes taylori occurs with a single host, *Lasius pallitarsis* (Provancher). Since the trichomes of this beetle are known to be attractive to the host, a study was initiated to determine the structure of gland cells presumed to be associated with the trichomes.

¹Scientific paper number 4518. Joint contribution by the Department of Entomology and the Electron Microscope Center, Washington State University, College of Agriculture Research Center. Work done under Project 0037.

²Senior Scientific Aide, and Entomologist and Professor, respectively, Department of Entomology, and electron microscopist, Electron Microscope Center, Washington State University, Pullman, Washington 99163.

³Current address, W. B. Hill, Tree Fruit Research and Extension Center, Wenatchee, Washington 98801.

Received for publication November 13, 1975.

A recent review of the structure of insect epidermal glands (Noirot and Quennedy, 1974) contains an extensive literature list of the subject. Gland cells described from the sex pheromone glands of male *Harporbitacus* (Crossley and Waterhouse, 1969), cells 2a + b in the defense glands of *Eleodes* (Eisner *et al.*, 1964), the cells comprising the pygidial glands of *Bledius* (Happ and Happ, 1973), and from the closely related *C. testaceus* (Kruger, 1910) are most similar in structure to the gland cells found in *A. taylori*.

METHODS AND MATERIALS

Tissue was exposed for fixation by cutting the pterothorax and abdomen into halves or quarters under a drop of cold fixative. Resulting pieces were maintained in ice-cold fixative for 2 hrs. The fixative used was 3% glutaraldehyde buffered with 0.1 M phosphate (pH 7.4). After washing, the tissue was post fixed for 1 hr in 2% osmium tetroxide buffered with 0.1 M phosphate buffer. Dehydration was in a graded series of ethanol. Pieces were embedded in Epon 812 (Luft, 1961). Sections were obtained with a Reichert OM-U3 microtome.

Three blocks were serially sectioned at 1–2 μ . Sections were stained with acid fuchsin and methylene blue (Huber *et al.*, 1968) and examined with a Nikon S-KE or Olympus Photomax light microscope using bright-field optics. These sections were surveyed to determine the type and location of any gland cells present.

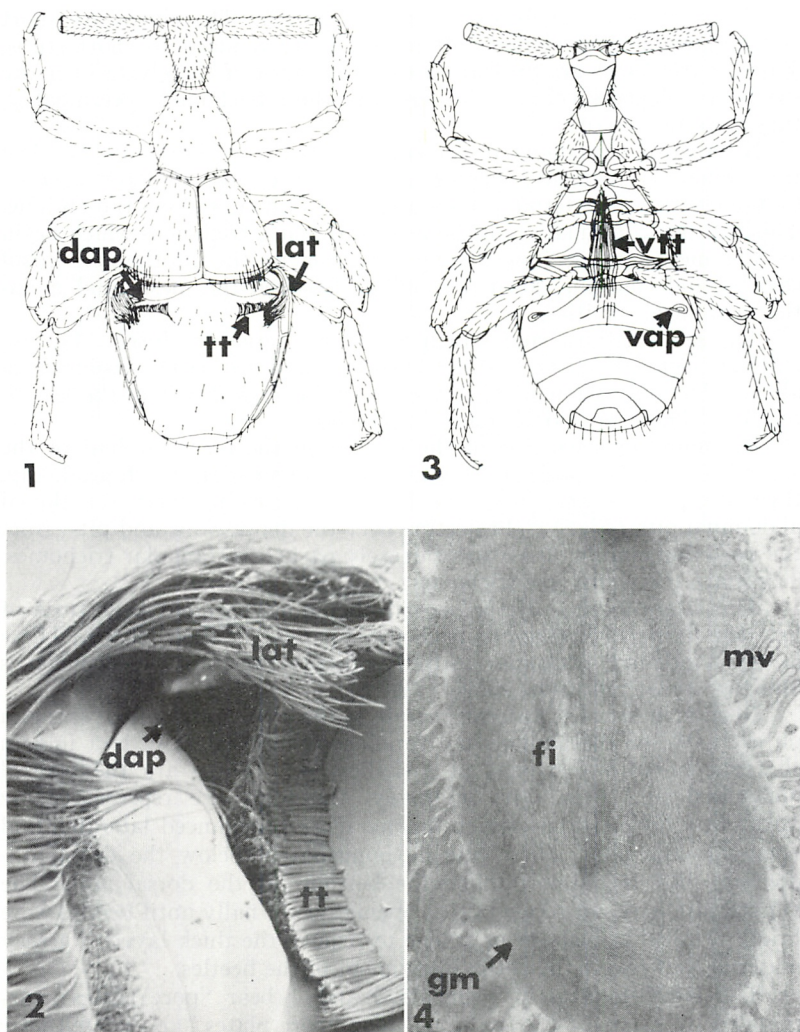
Sections for electron microscopy were initially cut at 2–2.5 μ , mounted on carbon coated glass slides, and coated with a thin layer of Epon. Sections were examined with the light microscope using phase contrast optics. Those sections selected for electron microscopic examination were cut from the Epon film and mounted on suitable stubs. This material was then cut at 60–80 nm and mounted on unsupported copper grids. Examination was in a Hitachi HS-8 or HU-125.

Contrast in these sections was enhanced by treatment with 0.5% aqueous uranyl acetate followed by treatment with lead citrate (Reynolds, 1963), or by treatment with lead citrate alone.

For examination of the cuticular parts of the secretory apparatus of the various gland cells, specimens were treated with hot KOH for 10–15 min. The terga and sterna of the thorax and abdomen were separated to expose the internal surface of the cuticle, dehydrated in a graded series of ethanol and critical point dried (Cohen *et al.*, 1968). This material was examined in an ETEC Autoscan R-I scanning electron microscope.

MORPHOLOGY OF *ADRANES TAYLORI*

A brief discussion of the morphology of the pterothorax and abdomen of *A. taylori*, especially the distribution of the trichomes, is necessary before describing the distribution and structure of the gland cells.

FIG. 1. *Adranes taylora* dorsal view.FIG. 2. Scanning electron micrograph of the lateral abdominal angle. 250 $\times$.FIG. 3. *Adranes taylora* ventral view.FIG. 4. Longitudinal section through the end sac of a type 1 cell. 29,980 $\times$.

KEY

dap, dorsal abdominal pit; fi, filaments; gm, granular mass; lat, lateral abdominal trichomes; mv, microvilli; tt, transverse trichomes; vap, ventral abdominal pit; vtt, ventral thoracic trichomes.

The beetles are small, ca. 2.5 mm in length. The elytra are short and immovable, the second pair of wings are reduced to short stubs. Tufts of trichomes are present on the outer apex of the elytra of many specimens. Some specimens did not have these trichomes; presumably, they were broken off.

Numbering of abdominal segments follows that of Park (1942). The first abdominal segment is narrow, and the tergum is completely covered by the elytra. The sternum bears a tuft of trichomes along the midline. This tuft is a continuation of the ventral thoracic trichomes which begin on the mesosternum immediately posterior to the prothoracic coxal cavities and continue down the midline between the meso- and meta-thoracic coxal cavities.

The second, third, and fourth abdominal terga are fused. The remaining segments curve sharply downward and are barely visible from above. The only remnant of segmentation in terga 2-4 is in the latero-tergites. There are no abdominal spiracles.

Beginning on each side of the midline in the posterior half of the second tergum, is a wide shallow transverse depression which gradually, then abruptly deepens near the lateral margins to form the dorsal abdominal pits (Fig. 1). Projecting over the depressions and pits, from the posterior margin, are rows of densely packed rectangular trichomes. These are the transverse trichomes.

The latero-tergites of the second abdominal segment bear tufts of less densely packed setae-like trichomes for most of their length. These lateral abdominal trichomes partially obscure the transverse trichomes and the dorsal pits from above (Fig. 2).

Beginning near the anterior margin of the second abdominal sternum on each side of the midline and running postero-laterally is a fold in the integument which ends in a shallow pit. These are the ventral abdominal pits (Fig. 3). Internally, the folds are represented by apparently hollow ridges which become more pronounced laterally, and open into the pits. These pits lie immediately below the dorsal abdominal pits and almost touch the bottoms of the dorsal pits. The ventral pits were not recognized as openings externally until beetles were briefly washed in benzene or xylene to remove the thick layer of greasy material that covers the entire integument of the beetles.

The latero-tergites of segments 3 and 4 bear "pore plates" surrounded by a small cuticular ridge. The "pore plates" are located near the anterior margin of the latero-tergites. These structures were not visible in scanning electron micrographs unless the specimens had been washed in a fat solvent and were not reported by Akre and Hill (1973).

STRUCTURE AND DISTRIBUTION OF GLAND CELLS IN THE PTEROTHORAX AND ABDOMEN

Six morphologically distinct types of gland cells were found in the pterothorax and abdomen. Four of the cell types are intimately asso-

ciated with various groups of trichomes. Two of these four, however, are also found throughout the general epidermis. A fifth cell type opens to the surface through the "pore plates" in latero-tergites 3 and 4. A sixth cell type is found in areas subject to friction and is probably lubricatory in function (Kruger, 1910; Pasteels, 1968). All six cell types are variations of a class 3 gland cell following Noirot and Quennedy (1974).

In a class 3 gland cell, the gland cell is penetrated by a cuticular apparatus which is connected to a cuticular ductule or canal that drains the gland cell. The ductule or canal is enveloped by the cell that secreted it. Usually, one gland cell is connected to one ductule cell. However, in some cases, an additional cell is found between the other two.

Gland Cell Type 1. These cells are generally distributed throughout the epidermis of the upper surface of the elytra, the sides of the thorax and abdomen, and the terga of the abdomen. They are concentrated, however, in the epidermis below the ventral thoracic trichomes with gland cells type 3a + b.

The cytoplasm contains a large number of mitochondria. A well developed system of agranular endoplasmic reticulum is present throughout the cytoplasm, few profiles of rough-surfaced reticulum are seen. There is also present a moderate amount of electron dense granular material scattered throughout the cytoplasm. These granules occur as clusters or rosettes and have an irregular profile. The granules are free ribosomes or glycogen. No elements of a Golgi complex were found. Few vacuoles are seen near the secretory apparatus of the cell.

The apical plasma membrane is invaginated and elaborated into short regularly spaced microvilli forming an extracellular vesicle. The vesicle is part of the end apparatus which functions to collect and transport the glandular product into the associated duct leading to the cuticular surface.

Within the vesicle is a vesicular organelle, the end sac. In the electron microscope the end sac appears as a fine granular mass which occasionally penetrates between the tips of the microvilli. The microvilli are usually separated from the end sac by a narrow gap (Fig. 4). The end sac is cuticular in nature or at least contains chitin as it survives treatment with hot KOH.

The lumen of the end sac is packed with long filaments ca. 0.01 μ diam oriented parallel to the long axis of the sac. The filaments extend beyond the sac into the short duct and end just below the outer surface of the cuticle (Fig. 5). The filaments have an electron lucid core giving them the appearance of tubules. They appear to arise within the granular mass and may completely penetrate the granular mass.

The end sac is connected to the surface by the short cuticular duct which arises within a depression of the inner cuticle and ends in a flange formed by multiple foldings of its walls (Fig. 6). The duct is formed of an apparently single layer of dense cuticle different in composition from the material forming the end sac.

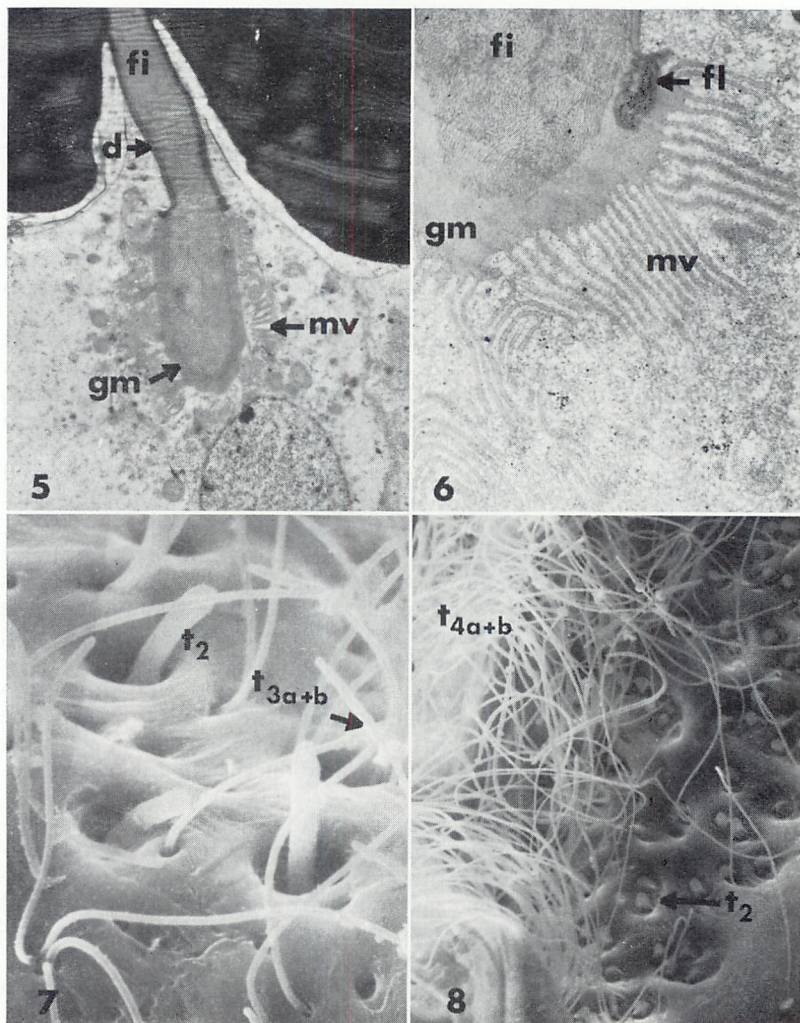


FIG. 5. Longitudinal section through a type 1 cell and its associated duct. 9,000 $\times$.

FIG. 6. Junction of end sac and duct of a type 1 cell. 33,000 $\times$.

FIG. 7. Scanning electron micrograph of the area below the transverse trichomes showing the cuticular remains of type 2 and 3a + b cells following treatment with KOH. 690 $\times$.

FIG. 8. Scanning electron micrograph of the area below the lateral abdominal trichomes showing the cuticular remains of type 2 and 4a + b cells following treatment with KOH. 1,414 $\times$.

Gland Cell Type 2. These cells are found below the transverse and lateral abdominal trichomes. The cells occur in groups with up to four arising from a single depression. Type 2 cells are associated with type 3a + b below the transverse trichomes (Fig. 7) and with type 4a + b below the lateral trichomes (Fig. 8).

The cytoplasm contains a large number of mitochondria. Profiles of agranular endoplasmic reticulum are seen throughout the cytoplasm. A moderate amount of granular material, free ribosomes or glycogen deposits, is present. Elements of a Golgi complex were not found and few vacuoles are seen in the cytoplasm.

As seen in Figs. 9 and 10, the end apparatus of these cells is similar to that of a type 1 cell. However, the end sac is larger and there is no flange at the junction of the duct and end sac (Fig. 10).

Gland Cell Type 3a + b. These cells are found generally distributed throughout the epidermis of the upper surface of the elytra, the sides of the thorax and abdomen, and the terga of the abdomen. These cells, like gland cell type 1, are concentrated in the epidermis below the ventral thoracic trichomes. They occur below the transverse trichomes with type 2 gland cells (Fig. 7), and are also concentrated along the ventral folds which end in the ventral abdominal pits (Fig. 11).

Each gland cell type 3a + b consists of a distal cell, 3a, a proximal or intercalary cell, 3b, a common vesicular organelle, a long efferent ductule, and an associated ductule secreting cell (Fig. 12).

The cytoplasm of a cell 3a contains a large number of mitochondria. An extensive system of flattened cisternae of granular endoplasmic reticulum occupies much of the volume of the cell. Occasional elements of Golgi complex are seen as are inclusions thought to be cytolysomes. A large amount of electron dense granular material, free ribosomes or glycogen deposits, is present. Numerous vacuoles containing a moderately dense granular textured material are seen in the vicinity of the end apparatus (Fig. 13).

The cytoplasm of a cell 3b contains many mitochondria. An extensive system of tubular agranular endoplasmic reticulum is present. A large amount of free ribosomes or glycogen deposits is present. Large deposits of lipid are present in the apical part of the cell.

The apical plasma membrane of a cell 3a is invaginated to form an extracellular microvilli lined vesicle. The vesicle itself is never clear. It contains a moderately electron dense granular material similar in texture to the contents of the vacuoles concentrated in the cytoplasm near the end apparatus (Figs. 12, 13). This material is probably the

←

KEY

d, duct; fi, filaments; fl, flange; gm, granular mass; mv, microvilli; T₂, cuticular remains of type 2 gland cells; t_{3a + b}, cuticular remains of type 3a + b gland cells; t_{4a + b}, cuticular remains of type 4a + b gland cells.

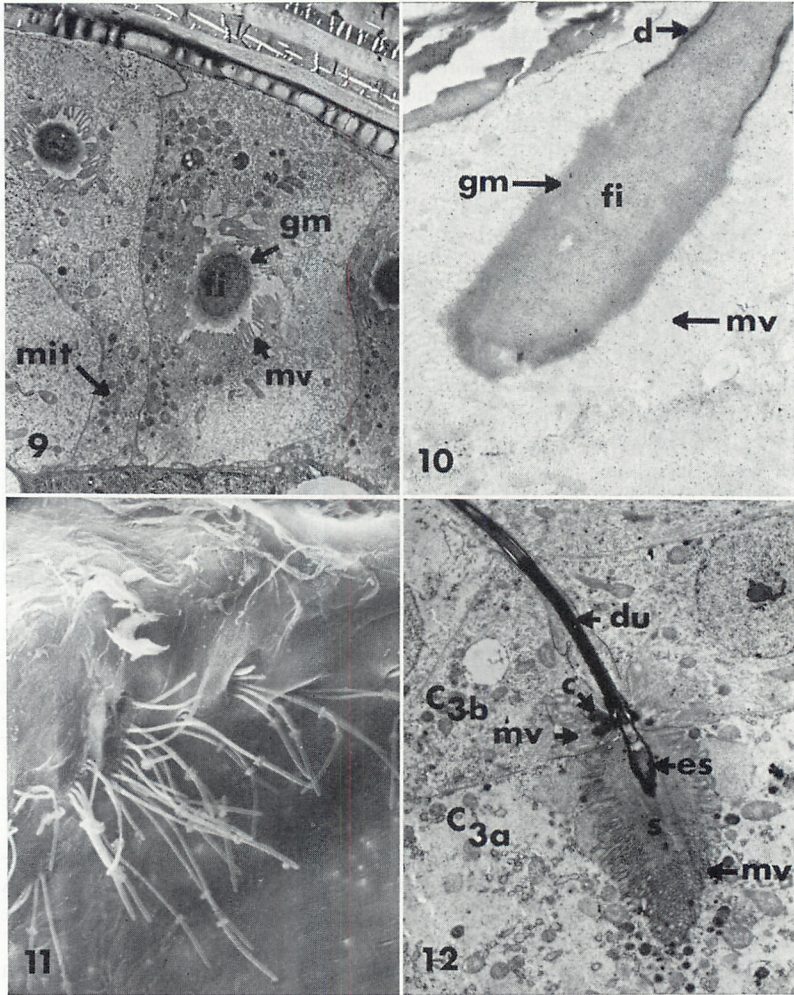


FIG. 9. Cross section through the end sac of three adjacent type 2 cells. 6,525 $\times$.

FIG. 10. Longitudinal section through a type 2 cell and its associated duct. 10,975 $\times$.

FIG. 11. Scanning electron micrograph of the area below the ventral fold showing the cuticular remains of type 3a + b cells. 1,400 $\times$.

FIG. 12. Section through a type 3a + b cell and its associated ductule. 8,600 $\times$.

KEY

c, collar; C_{3a}, cell 3a; C_{3b}, cell 3b; d, duct; du, ductule; es, end sac; fi, filaments; gm, granular mass; mit, mitochondria; mv, microvilli; s, secretion.

secretory product or its precursor. The lumen of the vesicular organelle also contains a similar appearing material. A granular material, representing secretion or its precursor, is present in the vacuoles surrounding the microvilli lined vesicle and in the vesicle of type 1 cells in the mycangium of *Dendroctonus* (Happ *et al.*, 1971).

The basal plasma membrane of a cell 3b is also invaginated and thrown into long, narrow, closely spaced microvilli. The vesicle thus formed is always clear.

The tips of the microvilli are separated from the vesicular organelle by only a narrow gap. The apical plasma membrane of this cell is invaginated to accommodate the efferent ductule and its secreting cell (Fig. 12).

The vesicles of cells 3a and 3b lie with their mouths in apposition (Figs. 12, 14). The apposing cell membranes are joined by septate desmosomes for much of their common length. Although this is not readily apparent in the micrographs, close examination of negatives with a binocular microscope shows the desmosomes are septate. Septate desmosomes also join the apposing membranes of cell 3b and the ductule secreting cell.

The vesicular organelle is divided into a terminal end sac which lies within the vesicle of cell 3a, a multilobed collar confined to the vesicle of cell 3b, and a short neck connecting the two (Fig. 15). The neck is closely bound by the plasma membrane of cell 3a above the vesicle of this cell, and by the plasma membrane of cell 3b below its vesicle (Fig. 14).

The end sac is composed of homogeneous cuticular material (resists treatment with hot KOH) and is ca. $3.7 \times .63 \mu$. The external surface of the sac is smooth, the luminal surface is irregular with many flattened processes projecting into the lumen. The sac is perforated by many small clusters of pores. A cluster of pores is associated with a luminal projection. This arrangement of pores is more clearly seen in micrographs of gland cells type 4a + b. Comparison of a number of sections through the end sacs of these two cell types indicates they are identical in this respect (Figs. 14, 16, 17).

Above the vesicle of cell 3a, the organelle is no longer porous and a thin, dense luminal layer is added. The inner layer is continuous with the layer forming the end sac but is thinner and slightly more dense at this point (Fig. 14). This is the neck.

The multilobed collar is composed of three layers. The two outer (luminal) layers are continuous with the layers of the neck. The inner layer is formed of a coarse granular material. Comparison of transmission and scanning electron micrographs shows this layer resists treatment with hot KOH and is cuticular. The lobes of the collar are extensions of the central lumen of the organelle. In some sections, the outer layers appear to be broken at the tips of the lobes.

Immediately above the collar the vesicular organelle is dome-shaped and is bound by the plasma membrane of cell 3b. Arising from the

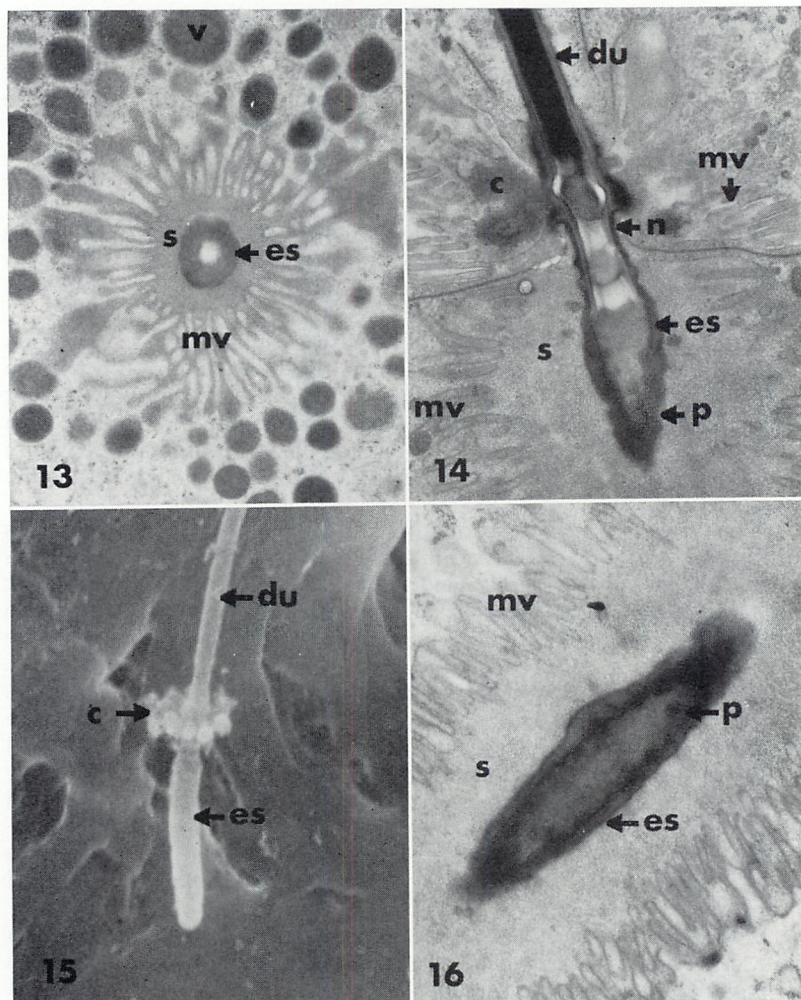


FIG. 13. Cross section through the end sac of a cell 3a. 22,340 $\times$.

FIG. 14. Section through a type 3a + b cell. 26,000 $\times$.

FIG. 15. Scanning electron micrograph of the vesicular organelle and ductule of a type 3a + b cell. 7,180 $\times$.

FIG. 16. Tangential section through the end sac of a cell 3a. 24,860 $\times$.

KEY

c, collar; du, ductule; es, end sac; mv, microvilli; n, neck; p, pores; s, secretion; v, vacuoles.

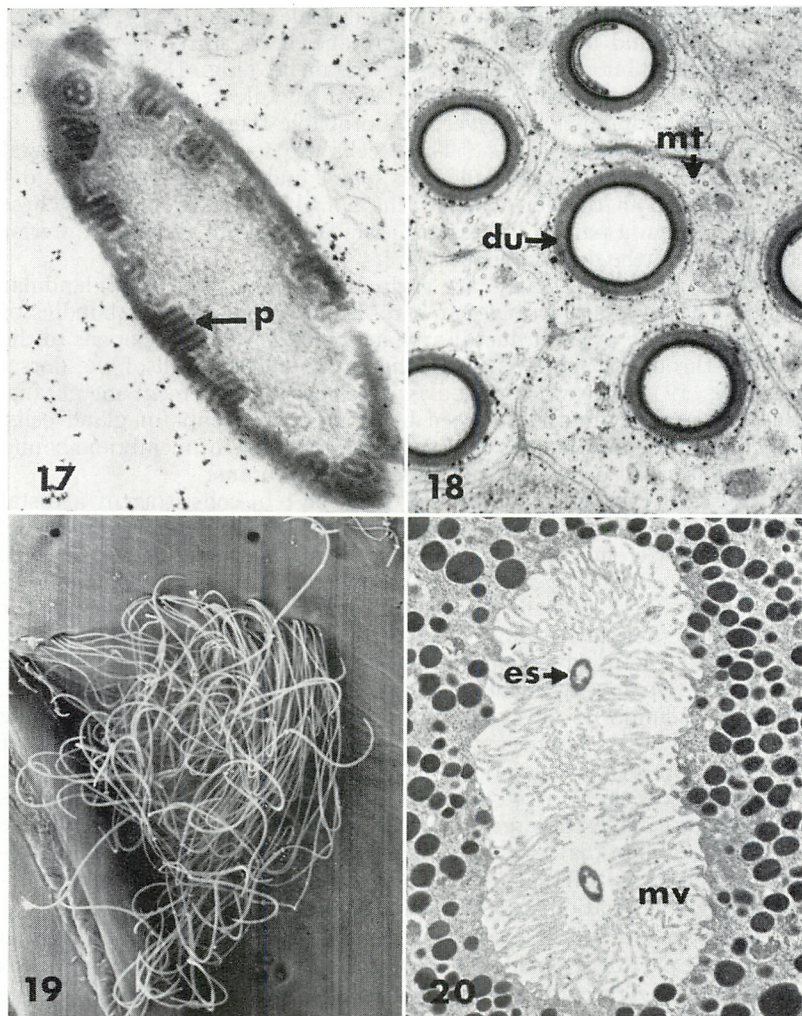


FIG. 17. Tangential section through the end sac of a cell 4a. 57,700 $\times$.

FIG. 18. Cross section through a group of ductule secreting cells associated with type 3a + b cells. 46,450 $\times$.

FIG. 19. Scanning electron micrograph of the area below the dorsal abdominal pit showing the cuticular remains of type 4a + b cells following treatment with KOH. 690 $\times$.

FIG. 20. Section through a type 4a cell. 8,300 $\times$.

KEY

du, ductule; es, end sac; mt, microtubules; mv, microvilli; p, pores.

center of the dome is the long efferent ductule (Figs. 12, 14, 15). The ductule is bound by the plasma membrane of its secreting cell and is thus extracellular as is the vesicular organelle (Fig. 18). It has not been possible to determine the number of ductule secreting cells associated with a ductule. However, it is probable there is only one.

Gland Cell Type 4a + b. These cells are found below the lateral abdominal trichomes with gland cells type 2 and a small group of 3 to 4 cells is found in the elytra below the apical elytral trichomes. These cells also form a pair of large glands which lie in the abdomen anterior and mesad of the dorsal abdominal pits.

These abdominal glands are each comprised of over 100 glandular units. The units are arranged in a rosette or acinus around bundles of centrally placed efferent ductules. Each bundle of ductules opens to the surface through a "pore plate" in the anterio-medial wall of the dorsal pit (Fig. 19). The whole gland is enveloped by basement membrane. Basement membrane is also seen between small groups of gland cells. Groups of efferent ductules corresponding to groups of membrane bound gland cells are also enveloped by basement membrane.

This cell type is similar to cell type 3a + b, consisting of a distal cell, 4a, a proximal or intercalary cell, 4b, a common vesicular organelle, and a long efferent ductule and associated ductule secreting cell or cells. The relationship between cells 4a, 4b, and the ductule cell and the relationship of these cells to the ductule and vesicular organelle appear identical to the relationships described for cell type 3a + b (Figs. 12, 20, 21). The structure and composition of the vesicular organelles of these cell types also appears identical (Figs. 12, 19, 20, 21, 22). In addition, there is a similarity in cytoplasmic organelles between corresponding cells in the two cell types. These cells are separated on the basis of size and the lack of secretion in the vesicle of cell 4a. The end sac within the vesicle of a cell 4a is ca. $36 \times .63 \mu$. Both the cell and its vesicular organelle are larger than cell 3a and its organelle. The vesicle of cell 4a, unlike that of cell 3a, is always clear. Apparently the secretion of cell 4a is different in chemistry from that of cell 3a and was extracted during fixation and embedding with the materials used.

Gland Cell Type 5. These cells form paired multicellular glands in the lateral part of segments 3 and 4 of the abdomen. Each gland opens to the surface through a "pore plate" in the anterior margin of the latero-tergites of the segment in which they are found.

Transmission electron micrographs of these cells were not obtained and little is known of their structure. An apical microvilli lined vesicle is present and contains a cuticular vesicular organelle. The vesicle, like that of cells 4a, is always clear. The cytoplasm contains numerous vacuoles filled with a dense material concentrated near the end apparatus. Scanning electron micrographs of the vesicular organelle and efferent ductule, following treatment with hot KOH (Fig. 23), show no external differentiation of vesicular organelle and ductule.

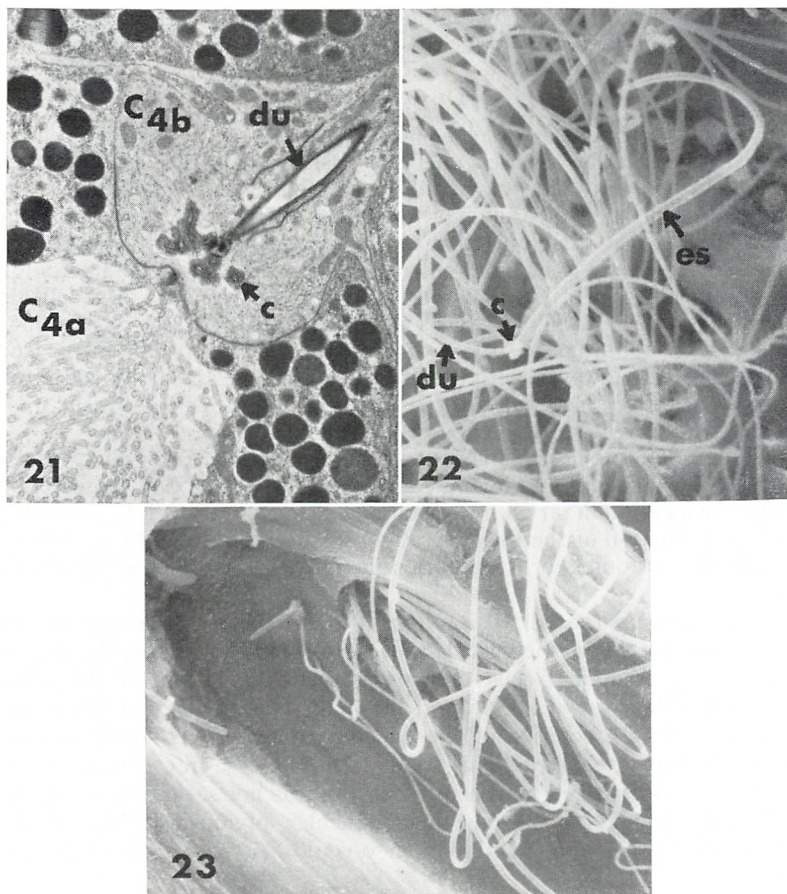


FIG. 21. Section through a type 4a + b cell. 19,000 $\times$.

FIG. 22. Scanning electron micrograph of the vesicular organelles and ductules of type 4a + b cells following treatment with KOH. 3,000 $\times$.

FIG. 23. Scanning electron micrograph of the area below a pore plate on a latero-tergite showing the cuticular remains of type 5 cells following treatment with KOH. 2,290 $\times$.

KEY

c, collar; C_{4a}, cell 4a; C_{4b}, cell 4b; du, ductule; es, end sac.

Gland Cell Type 6. These cells are found below the cuticle in areas subject to friction, being located in the coxae and coxal cavities and other movable joints. They were not examined with the electron microscope. However, examination with the light microscope indicates a gross structure similar to gland cell types 1 and 2, but somewhat longer and

frequently curved. They resemble those described by Kruger (1910) as lubricatory gland cells in a closely related pselaphid, *C. testaceus*.

DISCUSSION

Vesicular organelles of gland cells types 1 and 2 closely resemble that described from the sex pheromone secreting gland cells of male *Harpobittacus* (Crossley and Waterhouse, 1969). In *Harpobittacus*, the organelle is formed of a similar textured material. The lumen of the organelle is filled with long filaments which, in this case, penetrate the granular mass arising outside the end sac near the tips of the microvilli.

Filaments or fibrils are associated with the vesicular organelle in many class 3 gland cells (Mercer and Brunet, 1959; Eisner *et al.*, 1964; Filshie and Waterhouse, 1968; Gupta and Smith, 1969; Happ and Happ, 1970). However, with the exception of the filaments in cell types 1 and 2 described here and the cells described from *Harpobittacus*, filaments are not seen in the lumen of the organelle.

The function of these filaments is not known. Crossley and Waterhouse (1969) suggested they may act as a valve to the flow of secretion or be the location of structurally bound enzymes that mediate some step in the production of the final secretion. Eisner *et al.* (1964) postulated a selective trapping or transport function in the defense glands of *Eleodes*.

The duct associated with a class 3 gland cell is often secreted by a separate duct secreting cell. However, in some gland cells, the duct is secreted by epidermal cells that also secrete the intima of the gland reservoir (Happ *et al.*, 1966) or the main gland duct (Staddon and Thorne, 1973). Secretion of the duct by the gland cell itself has not been previously reported. This seems to be the case in cell types 1 and 2, although a duct cell may be present and was not seen. Class 3 gland cells are thought to secrete their vesicular organelles (Noirot and Quennedy, 1974) and it is likely they could also secrete the cuticular duct.

Association of different types and different classes of gland cells to form a gland or secretory epithelium also occurs in other insects. Two classes of gland cells are found in the mycangium of *Dendroctonus* (Happ *et al.*, 1971), and two types are found in the defense glands of *Eleodes* (Eisner *et al.*, 1964).

End sacs of cells 3a and 4a are unlike corresponding structures in other two-celled glandular units (Roth, 1943; Eisner *et al.*, 1964; Happ and Happ, 1973). Structurally, they most closely resemble the vesicular organelle of single-celled type 1 gland cells of *Dendroctonus* (Happ *et al.*, 1971) in lacking filaments and the thin outer layer often seen in the vesicular organelle of class 3 gland cells (Noirot and Quennedy, 1974).

The multilobed collar of cells 3b and 4b is unique morphologically.

The corresponding structure in cell 2b of *Eleodes* (Eisner *et al.*, 1964) is divided into a two-layered folded bellow and a larger spherical bulb, both fringed with filaments, while that in *Bledius* (Happ and Happ, 1973) is divided into a bulb and a long ductule like switchback region.

Although different in morphology, the collar appears similar in composition to the bulb in the medullary cell in *Bledius*. In *Bledius*, the bulb is composed of a mass of cylinders or filaments with open spaces in the filaments near the center. The bulb surrounds the central ductule and where the open spaces touch the ductule its inner layer is thinner and breaks occur in the outer layer.

The cytoplasm of the distal and proximal cells of gland cell types 3a + b and 4a + b contain different cytoplasmic organelles and it is obvious they synthesize different products. It is also apparent, from the relationship of a distal cell to a proximal cell and of the cells to their common vesicular organelle, the cells operate together in producing the final secretion.

Eisner *et al.* (1964) and Happ and Happ (1973) suggested the vesicular organelle may be a reaction chamber and, in a glandular unit composed of 2 cells, each cell contributes a different reactant or reactants. This hypothesis is supported by the studies of Happ (1968) on the synthesis of the secretion in the defense glands of *Eleodes*. An alternate hypothesis is that each cell contributes one or more components of a multi-component secretion (Happ and Happ, 1973).

CONCLUSIONS

Behavioral studies of *Adranes taylori* (Akre and Hill, 1973) and of other well integrated myrmecophiles and termitophiles (Holldobler, 1970; Pasteels, 1968; Seyfried, 1928; Kruger, 1910) have demonstrated the secretions of certain epidermal gland cells are attractive to and consumed by the host.

Epidermal gland cells associated with trichomes are found in a less well integrated myrmecophile, *Cremastochilus*. However, in this instance, the host ant is never seen touching the trichomes. Cazier and Mortenson (1965) believe the glands produce a volatile substance that makes the beetle attractive to the host with the result, the beetles are located and carried into the host nest. A volatile substance reputed to give the colony odor of the host to the inquiline is produced by certain epidermal glands in *Claviger testaceus* (Kruger, 1910). Although the secretions produced by the special epidermal glands of inquilines have not been identified and specific functions assigned to them, most authors consider them important to the host-inquiline relationship.

All the gland cells described from the pterothorax and abdomen of *A. taylori* are classified as class 3 gland cells following Noirot and Quennedy (1974). These cells represent 6 morphologically distinct types. Gland cell types 1 and 2 resemble, in the morphology of the vesicular organelle, the pheromone secreting gland cells of male *Harpo-*

bittacus (Crossley and Waterhouse, 1969). The vesicular organelle of gland cell types 3a + b and 4a + b are similar in several respects to the vesicular organelle of cells 2a + b in the defense glands of *Eleodes* (Eisner *et al.*, 1964) and in the cortical and medullary cells comprising the pygidial glands of *Bledius* (Happ and Happ, 1973). However, these 4 cell types are unique to *A. taylori* or at least to the Clavigerinae.

Kruger (1910) made the only previous study of the morphology of the glandular system of a clavigerine, *C. testaceus*. A comparison of Kruger's drawings and descriptions with the data from the present investigation suggests gland cell types 1, 2, 3a + b, 4a + b, and 6 are common to these two clavigerines. His "Myrmecophilendrus" II appears to represent gland cell types 1 and 2 of *A. taylori*, "Myrmecophilendrus" III represents gland cell type 3a + b. Gland cell type 4a + b is represented in *C. testaceus* by Wasmann's Gland which is similar in structure and location to the large paired glands comprised of cells type 4a + b that open into the dorsal abdominal pits of *A. taylori*. Gland cell type 6 is apparently represented by the grease glands in *C. testaceus*.

"Myrmecophilendrus" II and III are reported to produce a substance that is eaten by the host ant. Wasmann's Gland is reported to produce a volatile substance giving the beetle the colony odor of the host. Histochemical and further behavioral studies are needed to determine whether similar functions are performed by the analogous gland cell types of *A. taylori*. A reexamination at the fine structural level is also needed of the gland cells of *C. testaceus* to more adequately ascertain their morphological relationship to the gland cells described here.

Pasteels (1968) compared the epidermal glandular systems of termitophilous and free-living staphylinids. He found a primary system common to both groups and a secondary system different in each genus. Within the termitophilous genus *Termitella*, Pasteels found both hypertrophy and regression of parts of the primary system that he considers adaptations to termitophily.

A comparison of the glandular system of free-living and myrmecophilous pselaphids may indicate a similar evolution of the myrmecophilous glandular system in this family. Certainly, the presence of cell types 1 and 3a + b throughout the general epidermis and their concentration below various groups of trichomes suggests these concentrations may represent a hypertrophy of dermal glands (an element of Pasteels primary glandular system) which are present in the general epidermis of many insects.

ACKNOWLEDGMENTS

Sincere appreciation is extended to Dr. Carl A. Johansen and Dr. John W. Crane for critically reading the manuscript. Dr. R. Oetting is thanked for his many helpful suggestions throughout the study.

Acknowledgment is made to Dr. Arthur L. Cohen, Director, Electron Microscope Center, for his untiring support and interest in this project.

LITERATURE CITED

- Akre, R. D., and W. B. Hill. 1973. Behavior of *Adranes taylora*, a myrmecophilous beetle associated with *Lasius sitkaensis* in the Pacific Northwest (Coleoptera: Pselaphidae; Hymenoptera: Formicidae). J. Kansas Ent. Soc. 46:526-536.
- Cazier, M. A., and M. A. Mortenson. 1965. Bionomical observations on myrmecophilous beetles of the genus *Cremastocheilus* (Coleoptera: Scarabaeidae). J. Kansas Ent. Soc. 38:19-44.
- Cohen, A. L., D. P. Marlow, and G. E. Garner. 1968. A rapid critical point method using fluorocarbons ("Freons") as intermediate and transitional fluids. J. Microscopie 7:331-342.
- Crossley, A. C., and D. F. Waterhouse. 1969. The ultrastructure of a pheromone-secreting gland in the male scorpion-fly *Harporhynchus australis* (Bittacidae: Mecoptera). Tissue & Cell 1:273-294.
- Eisner, T., F. McHenry, and M. Salpeter. 1964. Defense mechanisms of Arthropods. XV. Morphology of the quinone-producing glands of a tenebrionid beetle (*Eleodes longicollis* Lec.). J. Morph. 115:355-399.
- Filshie, B. K., and D. F. Waterhouse. 1968. The fine structure of the lateral scent glands of the green vegetable bug *Nezara viridula* (Hemiptera, Pentatomidae). J. Microscopie 7:231-244.
- Gupta, B. L., and D. S. Smith. 1969. Fine structural organization of the spermatheca in the cockroach, *Periplaneta americana*. Tissue & Cell 1:295-324.
- Happ, G. M. 1968. Quinone and hydrocarbon production in the defensive glands of *Eleodes longicollis* and *Tenebrio castaneum* (Coleoptera, Tenebrionidae). J. Insect Physiol. 14:1821-1837.
- , and C. M. Happ. 1970. Fine structure and histochemistry of the spermathecal gland in the mealworm beetle *Tenebrio molitor*. Tissue & Cell 2:443-466.
- . 1973. Fine structure of the pygidial glands of *Bledius mandibularis* (Coleoptera: Staphylinidae). Tissue & Cell 5:215-231.
- , and S. J. Barras. 1971. Fine structure of the prothoracic mycangium, a chamber for the culture of symbiotic fungi, in the southern pine beetle, *Dendroctonus frontalis*. Tissue & Cell 3:295-308.
- Happ, G. M., J. D. Strandberg, and C. M. Happ. 1966. The terpene producing glands of a phasmid insect. Cell morphology and histochemistry. J. Morph. 119:143-159.
- Holldobler, B. 1971. Communication between ants and their guests. Sci. Amer. 224:86-93.
- Huber, J. D., F. Parker, and G. F. Odland. 1968. A basic fuchsin and alkalized methylene blue rapid stain for epoxy-embedded tissue. Stain Technology 43: 83-87.
- Jordon, K. H. C. 1913. Morphologie und Biologie der myrmecophilen Gattungen *Lomechusa* und *Atemeles* und einiger verwandter Formen. Z. Wiss. Zool. 107:346-386.
- Kruger, E. 1910. Beitrage zur Anatomie und Biologie des *Claviger testaceus* Preysl. Z. Wiss. Zool. 95:327-389.
- Luft, J. 1961. Improvements in epoxy resin embedding methods. J. Biophys. Biochem. Cytol. 9:409-414.
- Mercer, E. H., and P. C. J. Brunet. 1959. The electron microscopy of the left colleterial gland of the cockroach. J. Biophys. Biochem. Cytol. 5:257-262.
- Noirot, C., and A. Quennedy. 1974. Fine structure of insect epidermal glands. Ann. Rev. Ent. 19:61-80.
- Park, O. 1942. A study in Neotropical Pselaphidae. Northwestern Univ. Stud. Biol. Sci. and Med. 1:1-403.
- Pasteels, J. M. 1968. Le systeme glandulaire tegumentaire des Aleocharinae (Coleoptera, Staphylinidae) et son evolution chez les especes termitophiles du genre *Termitella*. Arch. de Biol. 70:382-467.
- , and D. H. Kistner. 1970. A taxonomic revision of the termitophilous subtribe Perinthina (Coleoptera: Staphylinidae). I. The genera *Paraperin-*

- thus, *Perinithodes*, and *Physoperinthus* with a discussion of their integumentary glands and their relationships. Ann. Ent. Soc. Amer. 63:546-562.
- Reynolds, E. S. 1963. The use of lead citrate at high pH as an electron opaque stain in electron microscopy. J. Cell Biol. 17:208.
- Roth, L. M. 1943. Studies on the gaseous secretion of *Tribolium confusum*. Ann. Ent. Soc. Amer. 36:397-424.
- Seyfried, A. P. 1928. An anatomical-histological study of the myrmecophilous histerid *Chrysotaerius iheringi* Reichensp. Contributions to Myrmecophily No. 2. Thesis, Univ. Fribourg, Switz. 64 p.
- Staddon, B. W., and M. J. Thorne. 1973. The structure of the metathoracic scent gland system of the water bug *Ilyocoris cimicoides* (L.) (Heteroptera: Naucoridae). Trans. R. Ent. Soc. London 124:343-363.
- Wilson, E. O. 1971. The Insect Societies. Belknap Press of Harvard Univ., Press, Cambridge, Mass. 548 p.